Theor Appl Genet (1997) 94:612–618

I. Karsai · K. Mészáros · P. M. Hayes · Z. Bedő

Effects of loci on chromosomes 2 (2H) and 7 (5H) on developmental patterns in barley (*Hordeum vulgare* L.) under different photoperiod regimes

Received: 1 August 1996 / Accepted: 15 November 1996

Abstract Heading-date in cereals is the final result of a number of interacting characters that include vernalization requirement, photoperiod sensitivity, and earliness *per se*. Progress in developing adapted varieties may be achieved by determining the chromosomal locations of genes controlling these characters. Nineteen doubled-haploid (DH) lines from the *Dicktoo* × *Morex* mapping population were phenotyped in controlled-environment photoperiod experiments to determine the role of two previously detected QTLs on the developmental patterns of barley. The QTLs are hypothesised to represent the effects of the *Ppd* and *Sh2* loci on chromosomes 2 (2H) and 7 (5H), respectively. Alleles at the *Ppd* locus were found to be vary in response to photoperiod duration. Vernalization had some effect on alleles at both loci. The presence of early and late-flowering transgressive segregants in this mapping population can be explained by interactions between the *Ppd* and *Sh2* loci. The *Ppd* and *Sh2* loci are hypothesised to be homoeologous with the *Ppd* and *Vrn1* loci of wheat.

Key words Barley · Photoperiod · Vernalization · QTLs · Homoeology

Introduction

Heading-date in cereals is the final result of a number of interacting characters that include vernalization requirement, photoperiod sensitivity, and earliness *per se*. Progress in developing varieties adapted to particular environments may be achieved by determining the chromosomal locations of genes controlling these characters. Heading-date genes have been studied extensively using the techniques of classical genetic analysis. In this way, Takahashi and Yasuda (1970) proposed that three major genes (*sh*, *Sh2* and *Sh3)*, located on chromosomes 4, 7, and 5 respectively, are responsible for winter vs spring growth habit in barley. A multiple allelic series at the *Sh2* locus, and epistatic interactions among loci, were hypothesised to explain the range of growth habits seen in barley germ plasm (Takahashi and Yasuda 1970). Loci for photoperiod sensitivity have been extensively studied in wheat, where the *Ppd1*, *Ppd2* and *Ppd3* loci were mapped to chromosomes 2D, 2B and 2A respectively (Law et al. 1978). Barley chromosome nomenclature is currently in a state of transition. To facilitate reference to the barley genetics literature, we will use the traditional barley chromosome designations (1–7) in the remainder of this report. The recommended new nomenclature assigns barley chromosome numbers based on their homoeology with wheat. The equivalents are: 1 (7H); 2 (2H); 3 (3H); 4 (4H); 5 (1H); 6 (6H); 7 (5H).

Earliness *per se* has been extensively studied in barley. Four loci – *ea*, ea_{sp}, ea_c, ea_k, and *ea7* – were mapped to chromosomes 2, 3, 4, 5, and 6, respectively. These loci were found to control maturity and/or photoperiod sensitivity in spring barley (Nilan 1964; Takahashi and Yasuda 1970; Gallagher et al. 1991; von Wettstein-Knowles 1992). In addition, epistatic interactions were detected between loci within both the *ea* and *sh* series, and also between the two groups of loci (Gallagher et al. 1991). Doubled-haploid (DH) mapping populations allow for a systematic genetic characterisation of vernalization, earliness, and photoperiod sensitivity in barley (Hayes et al. 1993; Laurie et al. 1994; Pan et al. 1994; Laurie et al. 1995; Hayes et al. 1996).

The development of DH reference populations that can be repeatedly genotyped and phenotyped should

Communicated by J. W. Snape

I. Karsai (✉) · K. Mészáros · Z. Bedő
Agricultural Research Institute of Hungarian Academy of Sciences, Martonvásár, H-2462, Hungary

P. M. Hayes
Department of Crop and Soil Science, Oregon State University, Corvallis, OR 97331, USA

be of assistance in dissecting the genetic components of plant growth and development. In some cases, test populations may show discrete distributions of trait expression, allowing the genetic determinants to be mapped as single genes. In other cases, the determinants of trait expression must be mapped as quantitative trait loci (QTLs). Such QTLs may be attributable to the effects of a single locus, or to tightly linked loci. The two possibilities cannot be distinguished at the level of resolution afforded by most mapping populations. Based on the position of the QTLs relative to other markers, inferences can be made regarding candidate genes as the determinants of the QTLs. In this fashion, Pan et al. (1994) reported a large-effect heading-date QTL on the short arm of chromosome 2 and hypothesised that this QTL was due to the effects of alleles at the *ea* locus described by Nilan (1964). Similar results were reported in a different barley population by Laurie et al. (1994) and Laurie et al. (1995). These investigators identified this chromosome-2 locus as *Ppd-H1* and hypothesised that it was homoeologous with the *Ppd* loci on the group-2 chromosomes of wheat. Pan et al. (1994) also reported a large-effect QTL for heading-date on the long arm of chromosome 7, and this QTL was attributed to the segregation of alleles at the *Sh2* locus. Based on syntenic relationships and common markers employed in different test populations, Laurie et al. (1995) and Hayes et al. (1996) established comparable map positions for the *Sh2* and *Vrn1* loci in barley and wheat, respectively. Pan et al. (1994) demonstrated that the chromosome 2 and 7 heading-date QTLs interacted in an epistatic fashion. Based on evidence from comparative mapping in barley populations, and the synteny established among the *Triticeae* (Van Deynze et al. 1995), we hypothesise that the chromosome 2 and 7 heading-date QTLs reported by Pan in the *Dicktoo* × *Morex* population are effects of the *Ppd* and *Sh2* loci, respectively. We will use these locus designations in the remainder of this report. Alleles at these loci will be referred to as D and M, for *Dicktoo* and *Morex*, respectively.

Our objectives were to build on the available information regarding the genome position of two QTLs having significant effects on heading-date in the *Dicktoo* × *Morex* population by conducting extensive phenotypic assessments of specific genotypes from the population and using the methodology employed by Roberts et al. (1988) to define photoperiod sensitivity. Roberts et al. (1988) described a useful method for quantifying the developmental responses of plants to temperature and photoperiod using the reciprocal of the time taken from sowing to flower. The linear phase of this function simplifies the development of predictive equations and the characterisation of photoperiod sensitivity. Specifically, we studied the effects of alleles at the *Ppd* and *Sh2* loci on developmental phases of *Dicktoo*, *Morex* and 19 of their doubled-haploid (DH) progeny grown under photoperiod regimes ranging form 8-h light/16-h dark to continuous light.

Materials and methods

Nineteen DH lines representing the four possible marker genotype classes at the heading-date QTLs on chromosomes 2 and 7 reported by Pan et al. (1994) were identified in the *Dicktoo* × *Morex* barley mapping population. This DH population has been the subject of extensive mapping and QTL detection efforts (reviewed by Hayes et al. 1996). The molecular marker genotypes of these 19 lines were obtained from the 78-point data set used by Pan et al. (1994). In the case of chromosome 2, the target region was defined by the markers *ABC156*, *ABC170*, *CDO64*, and *ABC454*. The total distance between *ABC156* and *ABC454* is 27.4 cM. The heading-date QTL peak was located in the *ABC170–CDO64* interval (12.0 cM). On chromosome 7 the target region was identified by the markers *WG364*,*mR*,*Dhn1*, and BCD*265b*. These markers define a region of 37.6 cM. The heading-date QTL peak was located at *Dhn1– BCD265b* (13.0 cM). Regression was used to determine the phenotypic R^2 value for each marker locus, and combination of marker loci, on phenotype.

The 19 DH lines and the parents were phenotyped in a series of controlled-environment tests involving combinations of vernalization and photoperiod. In all cases the vernalization treatment consisted of 6 weeks of hardening seedlings at 6°C with an 8-h light/16-h dark photoperiod regime. Seedlings for the unvernalized treatments were established 1 week prior to the end of vernalization so that plant material from both treatments was transplanted at the same time, and at approximately the same growth stage. Photoperiod treatments consisted of 8-, 10-, 12-, 14-, 16-, 18-, and 24-h light regimes per 24-h period and were carried out in the phytotron facilities of the Martonvásár Research Institute (Martonvásár, Hungary) as described by Tischner (1993). These treatments will subsequently be referred to by the hours of light duration (8 h, 10 h, etc.), and a suffix indicating the vernalization treatment where v = vernalized and uv = unvernalized. The temperature was kept constant at 18°C day and night, and was the same for each treatment. Space limitations in the growth chambers limited the number of genotypes, and number of replications of each genotype, that could be assessed. We compromised with the 19 DH progeny and the two parents, with each genotype replicated twice. The experiment was designed so that both the unvernalized and the vernalized plants within a given photoperiod regime were placed in the same growth chamber. The following data were recorded on each experimental unit: number of days to appearance of the first main stem node [developmental phase 31 on Zadock's scale (Tottman and Makepeace 1979)] (DEV31); the number of tillers at DEV31; days to heading (developmental phase 49 on Zadock's scale) (DEV49); and plant height at DEV 49. The genotypic coefficient of photoperiod sensitivity at the different developmental phases was determined using the results from the linear portion of the response surface, which ranged from the 8–18 h photoperiod treatments, based on the formula of Roberts et al. (1988):

$$1/f = a + bP + cT,$$

in which f is the time from sowing to the given developmental phase, a and c are constants peculiar to the genotype, P is photoperiod (h/d), b is the genotypic coefficient of photoperiod sensitivity, and T is the mean diurnal temperature. Since the temperature was constant in the whole experiment, cT could be omitted from the equation. The b values presented in this report are shown $\times 10^3$.

Results

The controlled-environment tests provided a good measure of phenotype. For example, standard errors

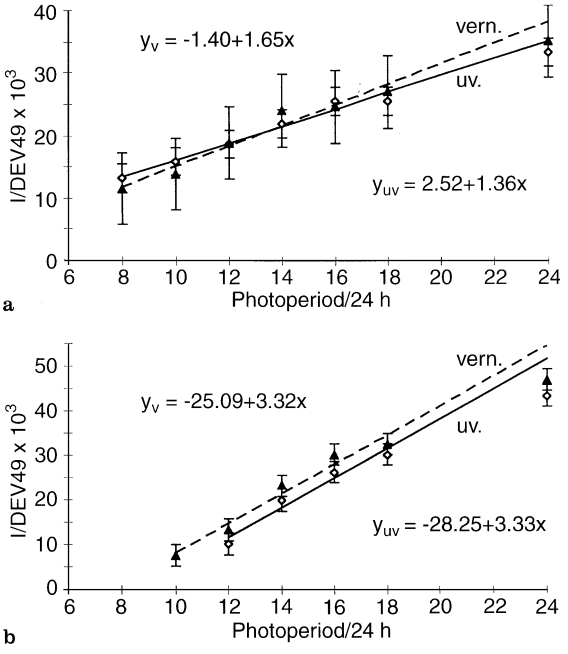

Fig. 1 Regression of 1/DEV49 on photoperiod regime, with and without vernalization, for the barley genotypes *Morex* (a) and *Dicktoo* (**b**). Standard-error bars are shown for each data point

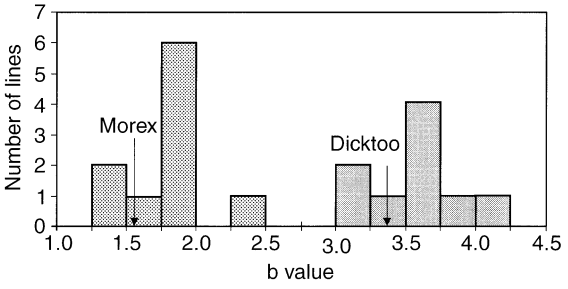

Fig. 2 Frequency distribution of photoperiod sensitivity (as defined in the text) for DEV49, averaged over vernalization treatments, for *Dicktoo*, *Morex* and 19 selected DH progeny

for 1/DEV49 for *Dicktoo* and *Morex*, with and without vernalization, are shown in Fig. 1. These figures underscore the much larger effect that photoperiod duration had on DEV49 than the vernalization treatment. Averaged over genotypes, photoperiod also had a greater effect on the time required to reach DEV31 than DEV49. DEV 31 was scored in these experiments as it is a good indirect measure of the turning-point from vegetative growth to the generative phase (Inagaki and Yasuda 1984).

As is apparent from the plots shown in Fig. 1, critical photoperiods (the photoperiod below which flowering is delayed) were not observed in *Dicktoo* or *Morex*. Rather, these genotypes, and their progeny, responded in a linear fashion to increasing photoperiod. No ceiling photoperiod (the photoperiod below which there is no additional delay in flowering) was found for *Morex*. In the course of this experiment, *Dicktoo* did not flower at photoperiods of less than 12 h.

In addition to establishing ceiling and critical photoperiods, plotting the reciprocal to the time to flower (1/DEV49), or time to reaching other development stages, allows one to readily describe the linear response of a genotype to increasing photoperiod with a single statistic: the slope of the line (b). The more responsive a genotype is to longer photoperiods, the higher the b value. Higher b values were obtained for *Dicktoo* than for *Morex* for both DEV31 and DEV49. For *Dicktoo*, b values averaged over vernalization treatments were 3.91 for DEV31, and 3.32 for DEV49, while for *Morex* the corresponding values were 2.12 and 1.51, respectively. The distribution of b values for the DH lines showed two discrete groups, suggesting monofactorial inheritance of photoperiod response (Fig. 2). When b values were regressed on marker genotypes, the *CDO64* marker on the short arm of chromosome 2 accounted for 75% of the variation in photoperiod response in the unvernalized treatments and 80% in the vernalized treatments.

The effects on developmental phenotypes of alleles at marker loci on chromosomes 2 and 7 under a 18-h photoperiod are summarised in Table 1. In both the vernalized and unvernalized treatments, genotypes with *Dicktoo* alleles at chromosome-2 marker loci were significantly earlier to head than genotypes with *Morex* alleles at these loci. Without vernalization, the DDMM genotypes were significantly earlier to head than the DDDD genotypes. This interaction will be addressed later in this report. It is also apparent that the effect of the *Dicktoo* allele at the *Ppd* locus was to shorten the period between DEV31 and DEV49. Effects of the *Dicktoo* allele at the *Ppd* locus were first detected between 12- and 14-h photoperiods, and continued reduction of this interval was observed with increasing photoperiod.

At an 18-h photoperiod, the *Dicktoo* allele at the *Ppd* locus had a significant pleiotropic effect on reducing plant height in the vernalization treatment and a similar trend was apparent without vernalization. These shorter plants also tended to have fewer tillers, but differences were not consistently significant across the vernalized and unvernalized treatments (Table 1). The phenotypic correlations shown in Table 2 confirm the multiple effects of the *Ppd* locus on plant growth and development. The b values, as a measure of photoperiod responsiveness, were negatively correlated with plant height, tillering, DEV31 and DEV49 both with and without vernalization. The four measures of plant growth and development were positively correlated, and the correlations were highest without vernalization.

The *Sh2* locus was not as sensitive to changes in photoperiod as the *Ppd* locus, and was not a significant determinant of photoperiod response when b values

Table 1 Effects of loci on chromosome 2 (the *Ppd* locus) and chromosome 7 (the *Sh2* locus) on the development and photoperiod sensitivity of 19 selected DH lines derived from the cross of *Dicktoo* × *Morex* at an 18-h light/6-h dark photoperiod regime

Trait	Marker genotypes on chromosome 2[b] and 7[b]				Multilocus R^2 (%)	*Dicktoo*	*Morex*
	DDDD	DDMM	MMMM	MMDD			
DEV31 uv (days)	20.3b[c]	16.7c	20.8b	38.2a	92.4	25.0	21.0
DEV31 v (days)	17.8b	16.6b	18.3b	25.2a	89.2	18.0	16.5
DEV49 uv (days)	30.3c	24.5d	38.3b	55.0a	96.8	33.0	39.0
DEV49 v (days)	27.0c	26.0c	36.5b	41.7a	91.5	31.0	37.0
Tillers uv (no.)	6.3b	4.0b	5.3b	11.9a	82.1	13.0	6.0
Tillers v (no.)	2.3b	2.4b	3.0ab	5.2a	54.9	5.5	4.0
Plant height uv (cm)	42.2b	42.2b	49.8ab	53.7a	49.7	38.7	50.7
Plant height v (cm)	42.3b	41.0b	53.9a	53.9a	64.8	44.0	56.5

[a] For markers *CDO64-ABC454*
[b] For markers *Dhn*1- *BCD*265*b*
[c] Values with a different letter (a–c) within a row are significantly different at the $P \leqslant 0.05$ level, by *F*-protected LSD tests

Table 2 Phenotypic correlations among traits at an 18-h light/6-h dark photoperiod regime without vernalization (above the diagonal) and with vernalization (below the diagonal) in 19 DH lines derived from the cross of *Dicktoo* × *Morex*. Traits and the photoperiod sensitivity index are defined in the text

Trait	Plant height	Tillers	DEV31	DEV49	Photoperiod sensitivity (b value)
Plant height		0.61***	0.58**	0.61*	− 0.64***
Tillering	0.14		0.92***	0.89***	− 0.77***
DEV31	0.41	0.83***		0.97***	− 0.84***
DEV49	0.60**	0.74***	0.90***		− 0.90***
Photoperiod sensitivity (b value)	− 0.66***	− 0.67***	− 0.85***	− 0.92***	

Significant at $*P < 0.05$, $**P < 0.01$, and $***P < 0.001$ level, respectively

were used as measures of genotype photoperiod response. The effects of the *Sh2* locus are portrayed in Fig. 3, allowing for a direct comparison with *Ppd*. In Fig. 3, the R^2 values for the *Ppd* and *Sh*2 loci, as they affected each measure of growth and development, are plotted across photoperiods. This provides a dynamic view of gene expression, assuming that a higher R^2 value reflects the relative importance of the gene in determining trait expression at a defined photoperiod. As was shown in the preceding sections, the D allele at the *Ppd* locus was responsive to increasing photoperiod. In order of magnitude of the R^2 value, the *Ppd* locus was a significant determinant of DEV49, DEV31, tillering and plant height. The effects were fairly consistent at the 12- and 14-h photoperiods. At photoperiods less than 12 h, the *Ppd* locus was not a significant determinant of trait expression, except in the case of DEV49 without vernalization. Without vernalization at photoperiods of less than 10 h, nearly 60% of the phenotypic variation for DEV49 was accounted for by this locus and genotypes with the D allele were later flowering. Vernalization essentially negated the effects of this locus as a determinant of flowering date at the 8-h photoperiod. With and without vernalization, at 10 h, no phenotypic variation for DEV49 was accounted for by the *Ppd* locus, but beginning at 12 h, this locus began assuming an important role as a determinant of trait expression, accounting for nearly 80% of the variation in trait expression. With the exception of DEV49, the effects of the *Sh2* locus were generally not as large as those of the *Ppd* locus and they were less dependent on photoperiod or vernalization. For example, without vernalization and between 10- and 24-h photoperiods, the D allele never accounted for more than 60% of the variation in trait expression, and the effects were quite consistent across photoperiods. For DEV49, between 10- and 24-h photoperiods, the *Sh2* locus accounted for 20–40% of the variation in trait expression, whereas with vernalization, it accounted for approximately 20% of the variation in trait expression at photoperiods ranging from 12 to 24 h.

When the *Ppd* and *Sh2* loci were considered jointly, they accounted for nearly 90% of the phenotypic variation in DEV31 and DEV49 in both the vernalized and unvernalized treatments (Table 1). The two loci accounted for less of the phenotypic variation in tiller number, and vernalization had an effect on this character, with 82% of the variation explained in the unvernalized treatment but only 55% of the variation explained in the vernalized treatment. The *Ppd* and *Sh2* loci were important determinants of plant height, but as they accounted for only 60–65% of the variation in phenotypic variation, other loci were probably important determinants of trait expression. As is also apparent from Table 1, the individual effects of the *Ppd* and *Sh2* loci are overshadowed by their interactions. The allelic configurations DDMM and MMDD gave transgressive phenotypes.

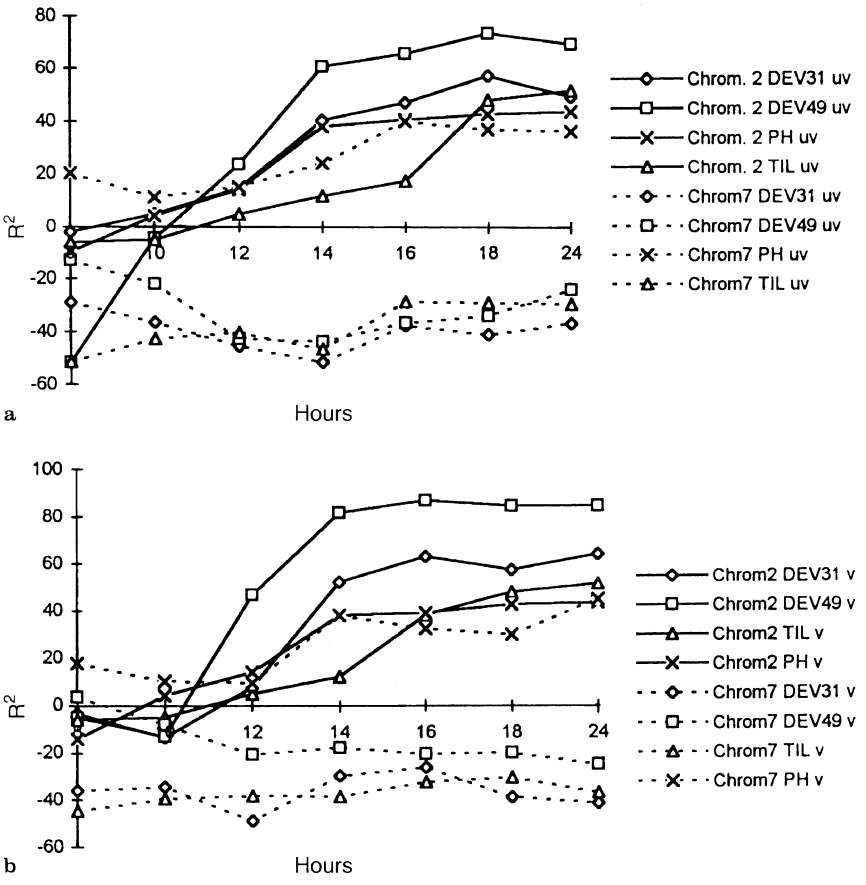

Fig. 3 The proportion of phenotypic variance (R^2) for growth and development traits accounted for by marker loci linked to the *Ppd* and *Sh2* loci in DH progeny of *Dicktoo* × *Morex*, without vernalization (**a**) and with vernalization (**b**). In each figure, data points on the plus-portion of the vertical axis indicate that the larger value allele was contributed by *Morex*, while values on the minus-portion of the axis indicate the larger value allele was contributed by *Dicktoo*

For example, the MMDD genotypes were significantly later in reaching DEV31 and DEV49 than any of the other genotypic classes and had a significantly higher number of tillers. They were not significantly different from the MMMM genotypes for plant height. The DDMM genotypes were significantly earlier to reach DEV31 and DEV49 than any other of the other genotypes without vernalization. Vernalization had little effect on them, whereas it did shorten the time required to reach DEV31 and DEV49 for the other genotype groups. As noted in the preceding sections, the effects of vernalization were not consistent. There were several instances where vernalization had an effect on the *Sh2* locus. For example, as shown in Fig. 3, with vernalization *Sh2* was not as significant a determinant of DEV49 as it was without vernalization. The influence of vernalization on the *Ppd* locus is apparent in Fig. 3 where, without vernalization, the D allele was a significant determinant of flowering at the 8-h photoperiod. With vernalization, the alleles at the *Ppd* locus were not significant determinants of DEV49.

Discussion

The methodology of Roberts et al. (1988) was useful in describing photoperiod sensitivity in this sample of lines from the *Dicktoo* × *Morex* population. Critical photoperiods could not be established in this germ plasm. A number of the genotypes studied by Roberts et al. (1988) also responded in a linear fashion to increasing photoperiod. The *CDO64–ABC170* interval on chromosome 2 defined a QTL peak for heading- date, according to Pan et al. (1994), and this QTL was attributed to segregation of alleles at the *ea* locus. The large portion of phenotypic variation in photoperiod sensitivity accounted for by the *CDO64* marker locus in this study supports our contention that in this region on chromosome 2 there is a locus that represents a homoeolog of the *Ppd* loci on the group-2 chromosomes of wheat (Law et al. 1978; Scarth and Law 1983; Laurie et al. 1994). Additional fine structure comparative mapping will be required for definitive proof. The response of genotypes in this study to longer photoperiods was attributable to the *Dicktoo* allele at the *Ppd* locus. Laurie et al. (1994) also reported that the winter barley genotype *Igri* had a photoperiod-responsiveness allele on chromosome 2 that caused earlier heading under long photoperiods. The effect of the D allele at the *Ppd* locus is to accelerate growth and development, and this acceleration proceeds in a linear fashion at photoperiod regimes with greater than 12 h of light per 24-h cycle. Genotypes with this allele accumulated fewer assimilates, leading to reduced plant height and, to some extent, reduced tillering. Laurie et al. (1994)

also reported pleiotropic effect of the *Ppd* locus on plant height, thousand-kernel weight, and plant-grain weight. Similar pleiotropic effect of *Ppd* loci were reported in wheat (Börner et al. 1993). While we have shown that the D and M alleles at the *Ppd* locus respond differentially to photoperiod duration, and that the response has a direct effect on plant growth and development, photoperiod sensitivity in the *Triticeae* remains a complex subject.

For example, Worland et al. (1994) surveyed a large collection of wheat germ plasms and reported that under long days, photoperiod-insensitive varieties flowered significantly earlier, and were shorter, than photoperiod-sensitive ones. This difference may be attributable to genes conferring what has been termed "earliness *per se*". Additionally, the allelic structure of their germ plasm at the *Ppd* loci was not reported. Data from other studies in wheat confirm the importance of genes that determine earliness *per se* and which can cause photoperiod-sensitive genotypes to flower earlier than photoperiod-insensitive ones (Martinic 1975; Hoogedoorn 1984). It is probable that photoperiod sensitivity is a complex character, resulting from interactions between loci differing in terms of their threshold photoperiod regime. In fact, some loci reported to determine earliness *per se* were shown to be photoperiod-dependent by Gallagher et al. (1991). To summarise the current perspective on photoperiod sensitivity in barley, the *Ppd* locus on chromosome 2 is activated at longer photoperiods, while the earliness *per se* loci, such as ea_{sp}, ea_c, and ea_k, are activated by shorter photoperiods (Yasuda 1977; Gallagher and Soliman 1988; Gallagher et al. 1991).

Plant growth and development, and ultimately heading-date, may be controlled, in large part, by loci that can be described as large-effect QTLs or Mendelian factors, such as the *Ppd* locus. However, interactions among loci are likely to be the rule rather than the exception, and the germ plasm studied in our experiments afforded an opportunity to study the interaction between the *Ppd* locus and the heading-date QTL on chromosome 7 described by Hayes et al. (1993) and Pan et al. (1994). We hypothesise that this QTL is due to allelic variation at the *Sh2* locus, based on the presence of markers in common between the *Dicktoo* × *Morex* population and the germ plasm studied by Takahashi and Yasuda (1970). At the *Sh2* locus, according to Takahashi and Yasuda (1970), there is a multiple allelic series that accounts for a gradation of growth habit from spring to winter. Based on comparative RFLP mapping, it is likely that the *Sh2* locus, in turn, is homoeologous to the *Vrn1* locus on chromosome 5 of wheat (Laurie et al. 1995; Hayes et al. 1996). A range of vernalization responses are present in winter barley germ plasm. The accession of *Dicktoo* used in our experiment does not have a vernalization requirement, in that under longer photoperiods, such as 18 h, it will flower within a few days of the spring parent (Table 1). However, as we have shown, *Dicktoo* and *Morex* have different alleles at the *Sh2* locus. If the *Sh2* and *Vrn*1 loci are indeed homoeologous, as we hypothesise, this lack of a vernalization requirement in *Dicktoo* my be attributable to the fact that it has one of a number of possible alleles at the multiple allelic series at the *Sh2* locus postulated by Takahashi and Yasuda (1970). Other winter barley genotypes would have alleles that are more vernalization responsive.

Pan et al. (1994) described the interaction between the chromosome-2 and the chromosome-7 heading date QTL in the *Dicktoo* × *Morex* population in terms of two-locus epistasis. The basis of this epistatic interaction is the independent assortment of alleles at the *Ppd* and *Sh2* loci that occurred in this winter × spring cross. The DDMM genotypes were earlier-heading than either parent under long photoperiods, due to a rapid appearance of the first-node, followed by a reduced period between first-node appearance and heading. The MMDD genotypes, in contrast, were slower to reach both growth stages and, as a consequence, were later to flower than either parent.

These experiments demonstrated the utility of marker-based analyses for identifying candidate loci that are determinants of heading-date QTLs in barley. They provided an insight into the complexity of photoperiod and vernalization response, and revealed the physiological basis of a two-locus epistatic interaction. Additional experiments are needed to determine the role of other heading-date genes in this germ plasm, and in other sources of barley germ plasm, and to unequivocally establish the identity of the *Ppd* and *Sh2* loci as the determinants of the chromosome-2 and -7 heading date QTLs in the *Dicktoo* × *Morex* population.

References

Börner A, Worland AJ, Plaschke J, Schumann E, Law CN (1993) Pleiotropic effects of genes for reduced height (*Rht*) and day-length insensitivity (*Ppd*) on yield and its components for wheat grown in middle Europe. Plant Breed 94:675–689

Gallagher LW, Soliman KM (1988) Classification of global environments and cultivars of spring barley based on heading-time reactions. Plant Breed 100:124–136

Gallagher LW, Soliman KM, Vivar H (1991) Interactions among loci conferring photoperiod insensitivity for heading-time in barley. Crop Sci 31:256–261

Hayes PM, Blake TK, Chen THH, Tragoonrung S, Chen F, Pan A, Liu B (1993) Quantitative trait loci on barley (*Hordeum vulgare*) chromosome 7 associated with components of winter hardiness. Genome 35:1019–1025

Hayes PM, Chen FQ, Corey A, Pan A, Chen THH, Baird E, Powell W, Waugh R, Bedö Z, Karsai I, Blake T, Oberthur L (1997) The *Dicktoo* × *Morex* population: a model for dissecting the components of winter hardiness. In: Li PH, Chen T (eds) Plant Cold Hardiness. Plenum, New York, USA (in press)

Hoogendoorn J (1984) The basis of variation in date of ear emergence under field conditioning amongst the progeny of a cross between two winter wheat varieties. J Agric Sci Cambridge, 104:493–500

Inagaki M, Yasuda S (1984) Beginning of internode elongation in barley varieties. Jpn J Breed 34 : 191–196

Laurie DA, Pratchett N, Bezant JH, Snape JW (1994) Genetic analysis of a photoperiod-response gene on the short arm of chromosome 2 (2H) of *Hordeum vulgare* (barley). Heredity 72 : 619–627

Laurie DA, Pratchett N, Bezant JH, Snape JW (1995) RFLP mapping of five major genes and eight quantitative trait loci controlling flowering time in a winter × spring barley cross. Genome 38 : 575–585

Law CN, Sutka J, Worland AJ (1978) A genetic study of day-length response in wheat. Heredity 41 : 185–191

Martinic Z (1975) Life cycle of common wheat varieties in natural environments as related to their response to shortened photoperiod. Z Pflanzenzüchtung 75 : 237–251

Nilan RA (1964) The cytology and genetics of barley. Washington State University Press, Washington, USA

Pan A, Hayes PM, Chen F, Chen THH, Blake T, Wright S, Karsai I, Bedö Z (1994) Genetic analisys of the components of winter hardiness in barley (*Hordeum vulgare* L.). Theor Appl Genet 89 : 900–910

Roberts EH, Summerfield RJ, Cooper JP, Ellis RH (1988) Environmental control of flowering in barley (*Hordeum vulgare* L.). I. Photoperiod limits to long-day responses, photoperiod-insensitive phase and effects of low-temperature and short-day vernalization. Ann Bot 62 : 127–144

Scarth R, Law CN (1983) The location of the photoperiodic gene, *Ppd2*, and an additional genetic factor for ear-emergence time on chromosome 2B of wheat. Heredity 51 : 607–619

Takahashi R, Yasuda S (1970) Genetics of earliness and growth habit in barley. In: Nilan RA (ed) Barley genetics II. Proc 2nd Int Barley Genet Symp, Washington State University Press, pp 388–408

Tischner T (1993) Lightning for plant growth in the Martonvasar phytotron. In: 7th European lightning conference, Heriot-Watt University Edinburgh, UK, pp 400–407

Tottman DR, Makepeace RJ (1979) An explanation of the decimal code for the growth stages of cereals, with illustrations. Ann Appl Biol 93 : 221–234

Yasuda S (1977) Linkage of the barley earliness gene *eak* and its pleiotropic effects under different growth condition. Berichte Ohara Inst fur LandwirtBiol, Okayama University 17 : 15–28

Van Deynze AE, Nelson JC, Yglesias ES, Harrington SE, Braga DP, McCouch SR, Sorrells ME (1995) Comparative mapping in grasses. Wheat relationships. Mol Gen Genet 248 : 744–754

Wettstein-Knowles P von, (1992) Cloned and mapped genes: current status. In Barley: genetics, biochemistry, molecular biology and biotechnology. Shewry PR (ed), CAB International, Oxford, pp 73–98

Worland AJ, Appendino ML, Sayers EJ (1994) The distribution in European winter wheats, of genes that influence ecoclimatic adaptability whilst determining photoperiodic insensitivity and plant height. Euphytica 80 : 219–228